REVIEW

Non-optimal animal movement in human-altered landscapes

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Summary

1. I synthesize the understanding of the relationship between landscape structure and animal movement in human-modified landscapes.

2. The variety of landscape structures is first classified into four categories: continuous habitat, patchy habitat with high-quality matrix, patchy habitat with low-quality matrix, and patchy, ephemeral habitat. Using this simplification I group the range of evolved movement parameters into four categories or movement types. I then discuss how these movement types interact with current human-caused landscape changes, and how this often results in non-optimal movement.

3. From this synthesis I develop a hypothesis that predicts the relative importance of the different population-level consequences of these non-optimal movements, for the four movement types.

4. Populations of species that have inhabited landscapes with high habitat cover or patchy landscapes with low-risk matrix should have evolved low boundary responses and moderate to high movement probabilities. These species are predicted to be highly susceptible to increased movement mortality resulting from habitat loss and reduced matrix quality.

5. In contrast, populations of species that evolved in patchy landscapes with high-risk matrix or dynamic patchy landscapes are predicted to be highly susceptible to decreased immigration and colonization success, due to the increasing patch isolation that results from habitat loss.

6. Finally, I discuss three implications of this synthesis: (i) 'least cost path' analysis should not be used for land management decisions without data on actual movement paths and movement risks in the landscape; (ii) 'dispersal ability' is not simply an attribute of a species, but varies strongly with landscape structure such that the relative rankings of species' dispersal abilities can change following landscape alteration; and (iii) the assumption that more mobile species are more resilient to human-caused landscape change is not generally true, but depends on the structure of the landscape where the species evolved.

Key-words: landscape structure, least cost path, dispersal ability, dispersal mortality, colonization

Introduction

Animals move for many reasons: to acquire resources; to avoid predators and other agents of mortality; to avoid competition (e.g. natal dispersal); and to be near conspecifics for mating and other social interactions (conspecific attraction). Clearly, the various functions of movement are related to survival and reproduction, and the parameters that govern movement are therefore subject to natural selection.

Movement parameters include the probability or per capita rate of leaving the current location (here called 'movement probability'), the distance moved (which combines movement speed and time spent moving), the probability of crossing boundaries between cover types when such boundaries are encountered, and the tortuosity of the movement path. Movement parameters may be plastic, depending on the physiological state of

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the organism (Bascompte & Vilà 1997; Bergman, Schaefer & Luttich 2000; Johnson *et al.* 2002; Fritz, Said & Weimerskirch 2003; Frair *et al.* 2005). For example, the movement path of a dispersing or migrating animal will usually be straighter, longer and less responsive to boundaries than the movement path of a foraging animal (Bergman *et al.* 2000; Frair *et al.* 2005; Dingle & Drake 2007).

In addition to the benefits of movement, movement entails costs in energy expenditure and increased mortality risk (Bélichon, Clobert & Massot 1996; Rothermel & Semlitsch 2002), and the cost of movement increases with the time spent moving (Baker & Rao 2004). Each movement choice made by an animal involves a balance between potential benefits and risks (Larsen & Boutin 1994). For example, the probability of leaving a protected site to obtain more resources depends on the trade-off between the risks of leaving, such as increased exposure to predation, and the benefits of leaving, such as higher quality and quantity of resources elsewhere than the current site (Mandelik, Jones & Dayan 2003; Brown & Kotler 2004; Schmitz 2005; Borcherding 2006).

The relative risks and benefits of different movement parameters also depend on the structure of the landscape where the animal is found. I define a landscape as a heterogeneous area, where the type and degree of heterogeneity depends on the species of interest (Fahrig 2005). Cover types within a landscape include habitat areas of varying quality, and non-habitat cover types presenting different risk levels to the animal. Many researchers have simplified this heterogeneity into a binary description of the landscape: habitat and matrix (non-habitat). Landscape structure affects movement parameters because different cover types in the landscape present different levels of risk and benefit (Johnson *et al.* 2002; Rothermel & Semlitsch 2002; Phillips *et al.* 2004; Belisle 2005; Hernandez & Laundre 2005). Since these risks and benefits vary among species, optimal movement parameters will be highly species-specific.

In this paper I first review current understanding of how movement parameters evolve in response to landscape structure. I simplify this by summarizing the variety of landscape structures into four categories, and the range of evolved movement parameters into four categories or movement types. I then discuss how these movement types interact with current human-caused landscape changes, and how this often results in non-optimal movement. From this synthesis I develop a hypothesis that predicts the relative importance of the different population-level consequence of these non-optimal movements, for the four movement types. Finally, I discuss implications of this synthesis and hypothesis for: (i) 'least cost path' analysis; (ii) testing ecological theories that involve 'dispersal ability'; and (iii) the common assumption that highly mobile species should be most resilient to anthropogenic landscape change. The arguments herein are made mainly in the context of actively moving animals, although some will apply to passive movement as well.

Evolution of movement parameters in response to landscape structure

MOVEMENT PROBABILITY

Many theoretical studies predict the evolution of optimal movement probability (usually termed 'movement rate') as a function of the risks and benefits of leaving the current site (Comins, Hamilton & May 1980; Levin, Cohen & Hastings 1984; Frank 1986; Klinkhamer *et al.* 1987; Paradis 1998; Dieckmann, O'Hara & Weisser 1999; Gandon & Rousset 1999; Ronce, Perret & Olivieri 2000; Heino & Hanski 2001; Hovestadt, Messner & Poethke 2001; Poethke & Hovestadt 2002; Cadet *et al.* 2003; Muller-Landau, Levin & Keymer 2003; Poethke, Hovestadt & Mitesser 2003; Parvinen 2006). The main benefits of movement are to avoid intra-specific competition, particularly kin-competition, in the current site, and to take advantage of under-exploited sites elsewhere. The main risk is mortality during movement. Several theoretical studies have predicted that the higher the probability of mortality during movement, the lower the movement probability that should evolve. On the other hand, increasing the probability of local population extinction through environmental stochasticity increases both the risk of remaining at the current site and the benefit of moving by increasing the chance of an emigrant finding an unexploited site. Therefore, higher rates of environmentally-driven local extinction select for higher movement probabilities. In an experimental microcosm study, Friedenberg (2003) showed that movement probability of a soil nematode increased with increasing rate of local extinction.

Theory also predicts that the balance between the risks and benefits of movement is affected by landscape structure, particularly the amount of habitat in the landscape, habitat patchiness, habitat permanence and matrix quality (mortality rate in the matrix) (Gadgil 1971; Paradis 1998; Travis & Dytham 1999; Ronce *et al.* 2000; Heino & Hanski 2001; Hovestadt *et al.* 2001). Species that evolved in landscapes with low amounts of patchy habitat should have higher movement probabilities if movement is less risky (the matrix is relatively benign) than if movement is risky. Species that evolved in landscapes with high habitat coverage should experience relatively low risk while moving, since most of their movements take place within the habitat. These species should evolve movement behaviours that respond mainly to local conditions rather than to potential risks of movement. For example, when access to conspecifics is important for breeding or other social interactions, an individual may choose to remain in the current site, but if a predator enters the site or the site becomes overcrowded, the individual may choose to move away. For these species the risks

associated with movement will have relatively little effect on movement probability.

Optimal per capita movement rate is also predicted to be higher, the more ephemeral the habitat is (Gadgil 1971; Paradis 1998; Travis & Dytham 1999; Roff & Fairbairn 2007), because ephemeral habitat should place a premium on escaping from existing habitat before it disappears, and on finding and exploiting new habitats as soon as they appear. For example, ballooning in spiders apparently represents a risk-spreading strategy as a response to habitat unpredictability (Bell *et al.* 2005). Denno *et al.* (1991) found larger proportions of moving individuals in planthopper species that occur in highly ephemeral habitats than in species from less ephemeral habitats. When movement mortality is high (low matrix quality) and habitat is ephemeral or local catastrophes produce frequent local extinctions, bimodal movement is predicted, with some individuals in the population showing a low tendency and others showing a high tendency to move (Travis & Dytham 1999; Parvinen 2006). Individuals with high movement tendencies may colonize newly available habitats but sustain a high probability of mortality en route, while individuals with low movement tendencies remain in and contribute offspring to local populations but risk dying out when their current habitat disappears. In the extreme this can lead to the evolution of two movement morphs, such as winged and wingless individuals, where the proportions can change depending on environmental conditions (Roff 1994; Roff & Fairbairn 2007).

BOUNDARY RESPONSE

When individuals are motivated to move, the decision of whether to make a particular movement may depend partly on whether, in moving, the animal must cross a boundary between cover types. Animals display a boundary response when they show either a tendency to remain in a patch when they encounter a patch boundary, or a preference to move into the cover type on the other side of the boundary (e.g. Kuussaari, Nieminen & Hanski 1996; Jonsen & Taylor 2000; Conradt, Roper & Thomas 2001; Ries & Debinski 2001; Collinge & Palmer 2002; Norberg, Enfjall & Leimar 2002; Schtickzelle & Baguette 2003; Davis & Stamps 2004; Hein, Poethke & Hovestadt 2005; Kuefler & Haddad 2006). The evolution of animal responses to boundaries has not been explicitly modelled. However, based on the theories for movement probability (above), it seems reasonable to predict that animals that evolved in landscapes with a risky matrix should often show a strong boundary response, leading them back into habitat when they encounter a habitat-matrix boundary. For example, planthoppers were more likely to move into a low-risk matrix type (brome) than a high-risk matrix type (mudflat) (Haynes & Cronin 2006). A butterfly species found in patches within a risky matrix showed a strong boundary response, while a congeneric species found in patches within a low-risk matrix readily crossed into the matrix (Kuras *et al.* 2003). The boundary response should be somewhat less pronounced for species in patchy, ephemeral habitats, because the ratio of the benefit of leaving the patch (finding a new one) relative to the risk of staying (the patch disappears) is higher than for species in patchy non-ephemeral habitats. As discussed above, such species often show a bimodal movement probability; the small proportion of animals that are committed to movement may then move irrespective of boundaries encountered. Animals that evolved in patchy landscapes with low-risk matrix, or in landscapes with continuous or nearly-continuous habitat, should show the lowest boundary responses. In the former case, the risk of crossing the boundary is low and in the latter case the frequency of encountering the boundary is low, so the selection pressure against crossing is low (Fig. 1). These predictions are supported in a study of movement patterns of a woodland butterfly (Merckx *et al.* 2003). Individuals from forested landscapes (continuous forest habitat) were more likely to cross the boundary from forest into open areas than were individuals from agricultural landscapes (patchy forest habitat). Note, however, that when an animal from continuous habitat enters a large patch of matrix, even though it is relatively insensitive to the boundary it may still 'change its mind' and return to habitat when it fails to encounter conspecifics or other resources in the matrix (Ries & Debinski 2001).

Animals that evolved in landscapes with patchy habitat and risky matrix should also evolve the ability to detect suitable habitat from a distance (e.g. Conradt *et al.* 2001; Hein *et al.* 2005). The probability of the animal crossing the habitat boundary and entering the matrix will then depend on the distance to suitable habitat, the ratio between the perceived quality of the currently occupied habitat and the distant habitat, and the risk level in the matrix. For example, forest birds and small mammals displaced across gaps in continuous forest choose a return route that minimizes distance travelled while balancing the risks of entering the gap vs. remaining in forest (Bélisle & Desrochers 2002; Bakker & Van Vuren 2004). The distance from which an animal can detect habitat will depend on the type of intervening matrix cover. Zollner & Lima (2005) suggest that in some situations, animals may be most able to detect new habitat across matrix types that have the highest predation risk. They argue that in this case the tendency to leave the habitat will be higher than predicted based on the matrix risk level alone.

CUE USE IN MOVEMENT DECISIONS

Dispersing animals and animals searching for resources often must make decisions about whether or not to move and/or whether or not to cross a boundary, without *a priori* knowledge of the actual risks and benefits of any particular movement choice. They may
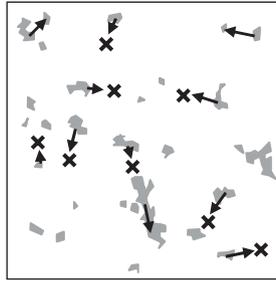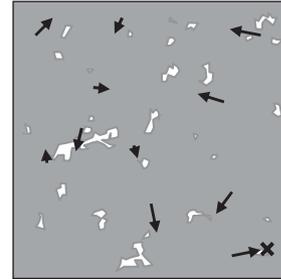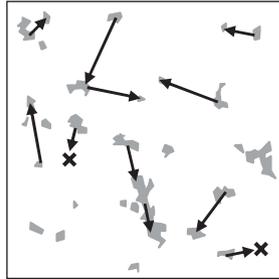
(a) High selection against crossing habitat boundary

Patchy habitat, low quality matrix

(b) Low selection against crossing habitat boundary

1. Patchy habitat, high quality matrix

2. Continuous habitat, low or high quality matrix

Fig. 1. Illustration of the effects of matrix quality and amount of habitat in the landscape on the selective pressure against crossing habitat boundaries into matrix (non-habitat). Shaded areas are habitat and white areas are matrix. Arrows represent individuals that are motivated to move away from their current site. X's represent individuals that died while attempting to move through the matrix to reach a new site. When habitat is patchy and the matrix is risky (a), movements across the habitat boundary into the matrix frequently result in mortality. In this situation there is strong selective pressure against leaving habitat, that is, strong selective pressure for a boundary response. In contrast, when the habitat is patchy and the matrix is not risky (b1), movement success is more likely and selection for a boundary response is weak. When the habitat is continuous, movements rarely result in encounters with boundaries and, when they do, the distance across the matrix is small. Here, movement success is generally high so, again, selection for a boundary response is weak.

not know in advance where the predators are lurking or where the best prey or other resources are located. However, the distributions of predators, resources, and conspecifics are not random; each is more likely to be found in some cover types than others. Natural selection acts on these correlations between cover type and risks and benefits to produce flexibility in movement parameters such that organisms use environmental indicators or cues in their movement choices. For example, without knowing the actual locations of host plants or prey items, animals preferentially move into cover types where the probability of finding their host plants and/or successfully capturing their prey is higher (Kunkel & Pletscher 2001; Rothermel & Semlitsch 2002; Cant *et al.* 2005; Gilby *et al.* 2006). Similarly, prey will avoid moving into habitat types in which predators typically lurk (Brown & Kotler 2004; Hopcraft, Sinclair & Packer 2005; Meerhoff *et al.* 2006) and will preferentially move into habitat types that provide protection from predation (Charland & Gregory 1995; Lauridsen & Lodge 1996; Grant & Brown 1998).

In addition to cover type, the presence of conspecifics in a patch can be used as a cue of habitat quality, so that animals are more likely to move into areas or less

likely to leave areas where conspecifics already occur (Stamps 1988; Lahaye, Gutierrez & Dunk 2001; Serrano & Tella 2003; Bowler & Benton 2005). Current population density or environmental conditions (e.g. day length) can also be used as cues of expected habitat quality. When population density or day length reaches a threshold, the probability of leaving increases sharply, in anticipation of reduced habitat quality; this is termed 'pre-emption' (Dingle & Drake 2007). Avoidance of kin-competition likely plays a role in such threshold responses to density. Similarly, some species use previous breeding performance as a cue to decide whether or not to remain in a particular area (Nager *et al.* 1996; Doligez, Danchin & Clobert 2002; Danchin *et al.* 2004; Sedgwick 2004). In an experimental study, Bondrup Neilsen (1993) showed that voles use their own condition as a cue to determine the risk/ benefit of moving.

PATH SHAPE

Optimal movement path shape differs within different cover types. When animals move through risky or low-resource cover types, their movement paths tend to be

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straight, which minimizes the time spent there (Crist *et al.* 1992; Stapp & Van Horne 1997; Schultz 1998; Mouillot & Viale 2001; Schultz & Crone 2001; Cant *et al.* 2005; Haynes & Cronin 2006). In contrast, movement paths in high-quality habitat are usually slower and more tortuous, which keeps the animal in the high-quality area (Shipley *et al.* 1996; Goodwin & Fahrig 2002; Nolet & Mooij 2002; Fortin 2003; Cant *et al.* 2005; Hein *et al.* 2005; Haynes & Cronin 2006). Note that the risks and benefits of different cover types will be different for different species in the same landscape, resulting in different movement paths for different species in the same landscape (Crist *et al.* 1992; Wiens *et al.* 1995; Etzenhouser *et al.* 1998; Norberg *et al.* 2002).

The effect of cover type on path tortuosity combines with the animal's boundary responses (above) and landscape structure to create different movement paths at the landscape scale (McIntyre & Wiens 1999a,b; With, Cadaret & Davis 1999; Hein *et al.* 2004). Animals with weak boundary responses are more likely to enter the matrix, where movement paths are straighter due to lower cover quality, so they will have less tortuous (straighter) paths at the landscape scale than animals with strong boundary responses.

MOVEMENT DISTANCE

Most of the theoretical studies on movement in landscapes predict how landscape structure should affect movement probability. Only a few make predictions about how landscape structure should influence optimal movement distance (Hovestadt *et al.* 2001; Murrell, Travis & Dytham 2002; Kallimanis *et al.* 2006). These assume that a longer movement distance reduces the level of intra-specific competition, particularly kin-competition, and increases the chance of finding unexploited resources, but also increases the animal's exposure to movement risks. Species that evolve in landscapes with high habitat cover are predicted to evolve longer movement distances than species that evolve in landscapes with low habitat cover, due to the lower movement cost per unit distance moved in habitat than in matrix. Movement distance is also predicted to vary with the spatial pattern of habitat and risks in the landscape. Spatial aggregation of habitat should favour shorter movement distances whereas spatial aggregation of risky cover types should favour longer movement distances (Kallimanis *et al.* 2006). When the habitat is patchy, there is selective pressure for movement distance to match the typical distances between habitat patches, thus maximizing movement success (Hovestadt *et al.* 2001; Muller-Landau *et al.* 2003; Hiebeler 2004). For example, Nürnberger (1996) found that pond-dwelling water beetles typically disperse distances that are similar to the distances between ponds. When resource quality is variable in space and time, species are expected to evolve a flexible movement distance, such that movement distance increases with decreasing reliability of

the benefits in the current patch. For example, foraging tundra swans move a long distance from a low-quality patch and a short distance from a high-quality patch (Klaassen, Nolet & Bankert 2006).

It is important to note, however, that the theoretical studies on movement distance to date represent movement as a simple passive process. None has yet evaluated optimal movement distance for animals exhibiting small-scale movement choices such as boundary responses and changes in path tortuosity in response to resource quality and risk (above). Such small-scale responses should scale up to affect realized movement distances. For example, animals showing strong boundary responses to stay within patchy habitat will have shorter movement distances than animals that readily move into the matrix. If animal movement is more tortuous in habitat than in matrix, movement distances in continuous habitat should be somewhat shorter than movement distances in patchy habitat with a high-quality matrix. Animals in continuous habitat are also more likely to find unoccupied, suitable habitat nearby than animals in patchy habitat, which again may result in somewhat shorter movement distances for animals that evolved in continuous habitat than animals that evolved in patchy habitat with high-quality matrix.

Non-optimal movement in altered landscapes

Over the past few decades, human activities have resulted in rapid, massive changes to landscapes: expansion of transportation networks; conversion of forest into grazing lands, agriculture and urban areas; draining of wetlands and damming and reconfiguration of waterways; and the introduction of various chemicals over large areas. Although some species show positive responses to some of these changes, for many species these changes can be summarized as: reductions in habitat quality and in the amount of high-quality habitat on the landscape; and reductions in the quality of the matrix (increased probability of mortality during movement in the matrix). In the rest of this paper I focus exclusively on this second category of species.

Since movement parameters evolve in response to landscape structure (previous section), when landscape structure changes, formerly optimal movement parameters may no longer be optimal. Given that movement parameters are under natural selection, one should expect them to evolve in response to landscape changes (e.g. Gandon & Rousset 1999; Heino & Hanski 2001; Muller-Landau *et al.* 2003). However, these landscape changes are ongoing, creating a moving target for the evolution of movement parameters. Whether or not a species' movement parameters are adaptive in the current landscape will depend on the rate of landscape change relative to the rate at which the species can evolve in response to that change. In some species with short generation times, traits related to movement have been shown to evolve within short

time periods. For example, wing size and body size in *Drosophila subobscura* (Gilchrist, Huey & Serra 2001; Gilchrist *et al*. 2004), and movement behaviour for predator escape in guppies (O'Steen, Cullum & Bennett 2002) evolved in less than two decades. It therefore seems likely that movement parameters of some species may be able to evolve fast enough to track landscape change if the selective pressure is strong enough.

Direct evidence for this suggestion is equivocal however. Taylor & Merriam (1995) found that damselfly wing sizes and thoracic weights were larger in landscapes where deforestation had occurred. They argued that microselection had occurred in these landscapes to allow damselflies to fly the farther distances between stream and forest habitats. Thomas, Hill & Lewis (1998) found similar results for a butterfly; relative allocation of mass to the thorax (as compared to the abdomen) increased with decreasing habitat amount, indicating higher flight capacity in landscapes containing less habitat. However, these differences may not represent local adaptations; instead they could indicate either phenotypic plasticity (Merckx & Van Dyck 2006) or that larger individuals are more likely to colonize isolated habitats (Hanski *et al*. 2004). In fact, in many species variation in movement parameters is largely environmentally controlled, so movement behaviour can change rapidly in response to changing conditions (Pulido 2007). However, whether or not this phenotypic plasticity will result in optimal movement choices in the face of changing landscapes depends on whether the species has encountered similar situations during its evolutionary history. A species with plastic movement responses may still 'misinterpret' a novel landscape cover type and display a non-optimal movement response to it (see below).

In many cases, changes to landscape structure are most likely occurring far too quickly for evolution of animal movement parameters to effectively track them (Remeš 2000; Thomas 2000; Pulido 2007). In simulation studies, it typically takes well over 100 generations for movement parameters to evolve to a new equilibrium in response to a sudden change in landscape structure (J. Travis, personal communication). Since landscapes are continually being changed by human activities, this suggests it is often impossible for evolution to track current landscape change through adaptations in animal movement parameters. In addition, since landscape change often involves habitat loss, resulting in smaller population sizes, the natural variability on which selection can act is reduced. This further curtails a species' ability to evolve in response to landscape change. Simulations by Paradis (1998) indicate that the more fragmented the habitat is, the longer it takes for movement probabilities to evolve; at least 1000 generations in highly fragmented landscapes.

Evidence suggests that the movement parameters of many species have not been able to track landscape change and have therefore become non-optimal. For example, for some species, typical movement distances match the historical density and distribution of resource patches. Where large-scale habitat loss has occurred these species may be unable to move between widely separated remnant habitat patches (e.g. Schultz 1998; Thomas 2000). Many animals also make inappropriate decisions to move and/or to cross boundaries in human-altered landscapes, because the landscape alterations have affected the actual correlations between landscape structure, and the risks and benefits of animal movement choices (Schlaepfer, Runge & Sherman *et al*. 2002; Remeš 2003). The mismatches between cues and the risks and benefits of cover types result in 'ecological traps', in which animals colonize low-quality human-altered habitats based on unreliable cues (reviewed in Robertson & Hutto 2006). For example, mayflies lay their eggs on roads, mistaking them for water (Kriska, Horváth & Andrikovics 1998). Some female turtles attempt to nest on gravel roadsides, thus increasing their susceptibility to road kill (Aresco 2005; Steen *et al*. 2006). Dragonflies mistake oil pools for breeding habitat (Horváth, Bernáth & Molnár 1998). Black-caps, cueing on early leafing shrubs, preferentially settle in a non-native black locust plantation rather then their natural habitat, even though their reproductive output is lower in the plantation (Remeš 2003). Chestnut-collared longspurs do not distinguish between native and exotic grasslands, even though nesting success is much lower in the exotic grasslands (Lloyd & Martin 2005). Indigo Buntings preferentially select patches with more edge, even though reproductive success is lower in these patches than in patches with less edge (Weldon & Haddad 2005).

While the ecological trap idea specifically refers to habitat selection, Schlaepfer *et al*. (2002) introduced the more general term 'evolutionary trap' to refer to any situation (including ecological traps) where the use of a formerly reliable cue has become maladaptive because of anthropogenic changes to the landscape. Evolutionary traps can occur at any point during animal movement, where the animal makes an inappropriate movement choice based on unreliable cues. For example, some species readily move onto roads, apparently equating them with open cover types in their natural environments (Ries & Debinski 2001; McDonald & St Clair 2004; Aresco 2005; Stevens *et al*. 2006). However, the risk of moving onto a road, particularly one with high traffic volume, is usually much higher than the risk of moving into other open cover types.

Non-optimal movement and population-level risks

In the section 'Evolution of movement parameters in response to landscape structure', I reviewed the relationships between landscape structure and the evolution of movement parameters. In the section 'Non-optimal movement in altered landscapes', I argued that anthropogenic landscape changes often result in non-optimal movement parameters. I now discuss the implications of this for population persistence. Figure 2 identifies
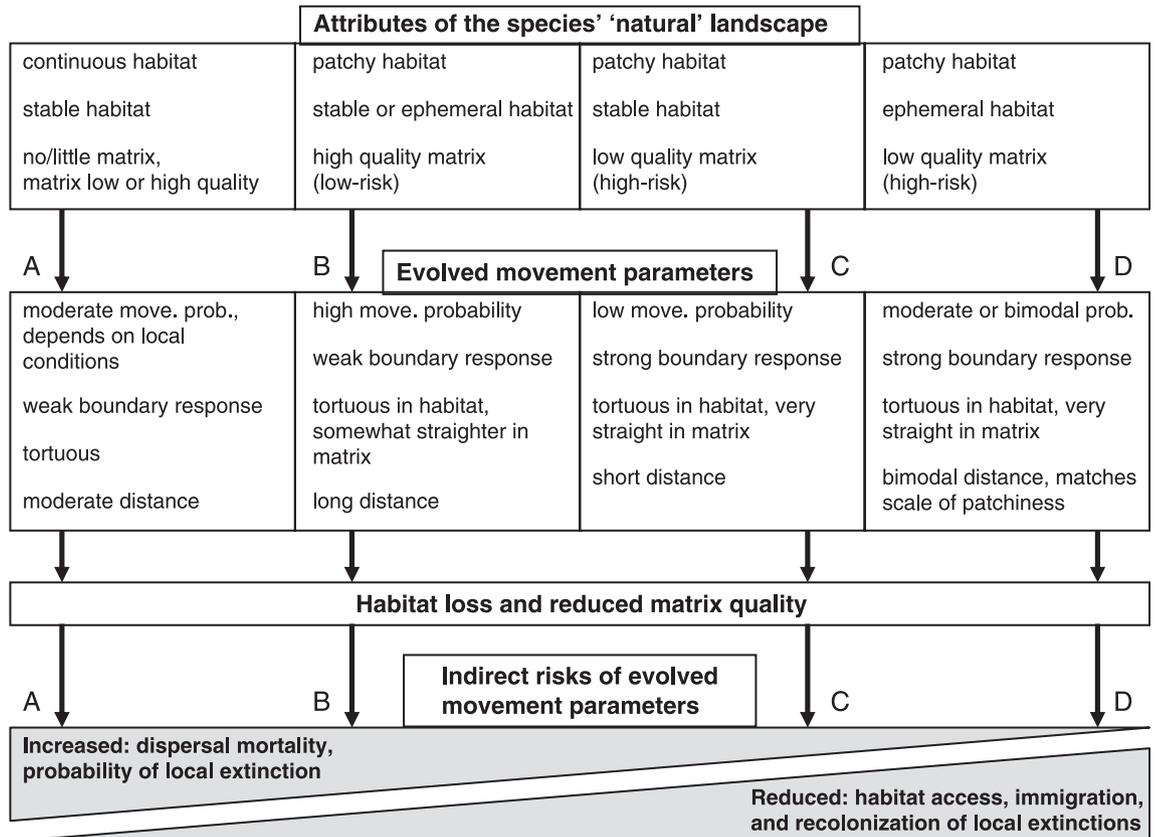
Attributes of the species' 'natural' landscape			
continuous habitat	patchy habitat	patchy habitat	patchy habitat
stable habitat	stable or ephemeral habitat	stable habitat	ephemeral habitat
no/little matrix, matrix low or high quality	high quality matrix (low-risk)	low quality matrix (high-risk)	low quality matrix (high-risk)

A ↓   B ↓ **Evolved movement parameters**   C ↓   D ↓

moderate move. prob., depends on local conditions	high move. probability	low move. probability	moderate or bimodal prob.
weak boundary response	weak boundary response	strong boundary response	strong boundary response
tortuous	tortuous in habitat, somewhat straighter in matrix	tortuous in habitat, very straight in matrix	tortuous in habitat, very straight in matrix
moderate distance	long distance	short distance	bimodal distance, matches scale of patchiness

↓ ↓ ↓ ↓

Habitat loss and reduced matrix quality

A ↓   B ↓   **Indirect risks of evolved movement parameters**   C ↓   D ↓

Increased: dispersal mortality, probability of local extinction

Reduced: habitat access, immigration, and recolonization of local extinctions

Fig. 2. Summary of the ideas presented in this paper, represented as four scenarios. The type of landscape in which a species evolves determines its evolved optimal movement parameters. These movement parameters combine with human-caused landscape changes to produce different population-level risks to different species. Populations of species that evolved in landscapes with high habitat cover (scenario A) or in patchy landscapes with low-risk matrix (scenario B) evolve low boundary responses and moderate to high movement probabilities. These species are highly susceptible to increased movement mortality resulting from habitat loss and reduced matrix quality. In contrast, populations of species that evolved in patchy landscapes with high-risk matrix (scenario C) or dynamic patchy landscapes with high-risk matrix (scenario D) are highly susceptible to decreased immigration and colonization success, due to the increasing patch isolation that results from habitat loss.

four contrasting natural (non-modified) landscape types. These four landscape types lead, through natural selection, to four contrasting species types, characterized by four sets of evolved movement parameters. These evolved movement parameters interact with human-caused landscape change to produce different risks to population persistence for the four species types. Note that many landscapes and species will not fit neatly into one of the four types in Fig. 2, since these four types represent the extremes of continua in landscape structure and movement parameters. As such, they allow us to understand the range of effects on population persistence that occur as a result of landscape change – habitat loss and reduced matrix quality – interacting with existing movement parameters. Here I discuss each of these types individually.

SPECIES EVOLVED IN CONTINUOUS HABITAT

Species that evolved in landscapes with high habitat amount should evolve a moderately high, flexible movement probability that depends on local conditions and is relatively insensitive to movement risk. They should also have low boundary responses (readily cross boundaries), because boundaries are infrequently encountered and, even if a boundary is encountered and crossed, the organism is likely to quickly encounter habitat again after moving only a short distance, due to the high abundance of habitat (Fig. 1). Therefore, the selective pressure on boundary responses will be low. Such species are at high risk from habitat loss, particularly when the habitat is replaced by a risky matrix cover type (Kindvall 1999; León-Cortés, Lennon & Thomas 2003). When habitat is removed, patch sizes go down and the amount of edge in the landscape goes up, so emigration rate increases, which increases overall movement mortality. Also, the distances between patches increase with decreasing habitat amount, which reduces movement success because of movement mortality (Hill, Thomas & Lewis *et al.* 1996; Baguette, Petit & Quéva 2000; Roland, Keyghobadi & Fownes 2000; Kindvall & Petersson 2000; Thomas 2000; Schtickzelle & Baguette 2003). Such species will travel into and through the matrix with little response to the actual risks there, which will increase the probability of population extinction (Gibbs 1998; Russell, Swihart &

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Feng 2003). In a simulation study, Tischendorf *et al.* (2005) showed that, once habitat loss has reached the point where the landscape contains less habitat than matrix, the lack of boundary response places such populations at risk. For animals with no evolved boundary responses, habitat loss adds a large component of movement mortality, which is not balanced by immigration.

SPECIES EVOLVED IN PATCHY HABITAT WITH HIGH QUALITY MATRIX (LOW MORTALITY IN THE MATRIX)

Species that evolved in patchy habitat with high quality matrix should have high movement probabilities and low boundary responses, readily moving through many cover types. Their movement distances should match the natural scale of habitat patchiness. Populations of these species will be particularly vulnerable to anthropogenic landscape changes that reduce matrix quality and remove habitat. Habitat loss will increase the amount of time that individuals spend in the matrix, where mortality risk has now increased. Therefore, movement mortality will be high and movement success will be low. In addition, per capita emigration rate will increase because habitat loss results in smaller patches with higher perimeter to area ratios. This will increase the probability of local extinctions. For example, some turtles are generally regarded as highly susceptible to human alterations of the landscape, due in part to their tendency to move indiscriminately through different cover types (Bowne & White 2004). Amphibian species that range widely over the landscape are more susceptible to forest loss and high road density than are less mobile species (Gibbs 1998; Carr & Fahrig 2001).

SPECIES EVOLVED IN PATCHY PERSISTENT HABITAT WITH LOW QUALITY MATRIX

Species that evolved in patchy habitat with risky matrix should have strong boundary responses. Movement probability should be low, just high enough to allow recolonization of local extinctions. Movement distances should be relatively short due to the high risk of movement. These species and type D species (below) are most likely to have evolved the ability to detect habitat from a distance; when the matrix is risky, the time spent there can be reduced if the animal knows exactly where it is going. For these species, habitat loss will reduce the likelihood of habitat occurring within the perceptual range of the organism, so habitat loss will further reduce the rate of movement out of patches. Habitat loss will also reduce the success rate of movement because the few animals that do move may not move far enough. Both of these effects will reduce resource accessibility, immigration rate and colonization rate. Habitat for these species will therefore not be fully occupied and empty patches will be common,

thus reducing the overall population size and increasing the extinction risk. On the other hand, a reduction in matrix quality will have relatively little effect on these species because emigration rates are already low due to naturally low matrix quality. These species are the ones for which corridors of habitat could work well to enhance population persistence through movement, because the animals will stay in the corridor, and the corridor will 'lead' them to the other habitat (Berggren, Birath & Kindvall 2002; Baum *et al.* 2004; Haddad & Tewksbury 2005).

SPECIES EVOLVED IN PATCHY DYNAMIC/ UNSTABLE/EPHEMERAL HABITAT WITH LOW QUALITY MATRIX

Finally, species that evolved in dynamic landscapes with low-quality matrix should evolve bimodal movement responses, with most of the population not moving, and the remainder of the population moving on the order of the typical distances between patches (Johst & Schöps 2003). Species with a bimodal movement strategy can be resilient to landscape change (e.g. Kotze & O'Hara 2003). However, habitat loss will increase the distance between patches, making the scale of movement non-optimal, which will reduce the colonization rate of new or recovered patches. This can have a strong negative effect on overall population persistence since colonization is critical in a system where patches disappear deterministically.

Implications

LEAST COST PATH ANALYSIS

There are several implications from the synthesis in Fig. 2. First, one should not assume that the movement choices made by animals are optimal or well-adapted in human-modified landscapes. While this may seem obvious, it is worth emphasizing this in the context of the increasing use of 'least cost path' analyses. These are computer algorithms that map estimated movement cost or 'resistance' surfaces and then find the least costly (or optimal) path for animal movement between patches or points on the landscape. Least cost path algorithms have been used to identify optimum movement routes for a wide range of organisms including birds, mammals, insects and amphibians (Bunn, Bunn & Keitt 2000; Ray, Lehmann & Joly 2002; Sutcliffe *et al.* 2003; Larkin *et al.* 2004; Kautz *et al.* 2006). However, there is a danger with the use of least cost path analyses in applied situations. Land-use decisions to protect optimum movement routes and allow development elsewhere implicitly assume that animals are able to make the 'correct' movement choices to find the least cost path. Given the recent and current rate of landscape change, this assumption is likely often incorrect. In their simulation study, Russell *et al.* (2003) demonstrated that population dynamics and distribution

are highly sensitive to this assumption. Land management based on this assumption could lead to inappropriate management decisions. Therefore, least cost path analysis should not be used as a substitute for data on actual movement paths and movement risk.

TESTING HYPOTHESES INVOLVING 'DISPERSAL ABILITY'

A recent search of the Web of Science revealed 830 papers using the term 'dispersal ability' or 'dispersal capability'. Animal dispersal is generally defined as movement from a natal to a breeding site, and dispersal ability refers to the ability of animals to make these movements. Dispersal ability has been proposed as an important predictor variable in a variety of ecological and evolutionary hypotheses. For example, dispersal ability has been hypothesized to affect: the relationship between biodiversity and ecosystem function (Zobel *et al.* 2006); species range size (Gaston 1996); the outcome of competition (Levins & Culver 1971; DeAngelis, Trexler & Loftus 2005); the speed of species invasion (Neubert & Caswell 2000); the rate of speciation (Gavrilets, Li & Vose 2000); and the relative importance of neutrality and niche partitioning in determining species abundance and distribution (Gravel *et al.* 2006). In these and other hypotheses involving dispersal ability, the underlying assumption is that dispersal ability is an attribute of a species, which can be estimated independently of its environment.

However, as discussed above, anthropogenic landscape change alters the ability of animals to move through landscapes. This means that the dispersal ability of a species is not simply an attribute of the species, but varies widely with landscape structure. In fact, since landscape changes have different effects on different species, the relative rankings of different species' dispersal abilities will also change as landscapes change. For example, a species of type B (Fig. 2) that evolved in an area of patchy habitat and high-quality matrix should evolve long movement distances. As argued above, such a species will be particularly vulnerable to increasing risks in the matrix, which will reduce its dispersal ability in modified landscapes. In fact, its dispersal ability in modified landscapes may be even lower than that of a species with a shorter innate movement distance (i.e. a lower dispersal ability in unmodified landscapes), such as a species that evolved in an area of patchy habitat and high-risk matrix (type C, Fig. 2). Therefore, if dispersal ability is assumed to be an attribute of a species independent of the landscape, hypotheses tested in very different landscapes will appear to fail.

As an interesting example of this, Ferraz *et al.* (2007) tested the hypothesis that forest patch isolation should more strongly reduce patch occupancy by species with low dispersal abilities than by species with high dispersal abilities. In contrast to this expectation, they found no effect of dispersal ability on the patch isolation effect. As a possible explanation, they suggested that species' dispersal abilities 'change in disturbed landscapes to the extent that we cannot use them to predict occupancy parameters under disturbance' (Ferraz *et al.* 2007). Therefore, to test a hypothesis involving dispersal ability, either: (i) the test location should be chosen carefully to match the type of landscape where the original dispersal ability data were collected; or (ii) the dispersal ability of the species or group of species in the test should first be empirically evaluated in the same landscapes where the hypothesis is to be tested.

MOBILITY VS. EXTINCTION RISK

This leads, finally, to the frequent assertion that more mobile species should be more resilient to anthropogenic landscape change than less mobile species (Hanski & Thomas 1994; Tscharntke *et al.* 2002; Grimm *et al.* 2004). This is based on the argument, originating in metapopulation modelling, that a more mobile species is better able to recolonize local extinctions and rescue populations from low numbers. However, this argument does not take into account the higher mortality rate that mobile organisms can experience, as they move into more hostile human-dominated cover types. This increase in movement mortality can lead to the exact opposite prediction, namely that more mobile species are more susceptible to population extinction in human-modified landscapes (Casagrandi & Gatto 1999; Fahrig 2001; Flather & Bevers 2002). As stated by Reinhardt *et al.* (2005): 'Individuals emigrating from habitat fragments may be unable to bridge non-habitat areas because their dispersal ability has evolved under a less fragmented structure of the landscape.' Since low movement probability does not allow recolonization and high movement probability entails high movement mortality, one might predict that an intermediate movement probability would be overall the strategy most resilient to landscape change (Casagrandi & Gatto 1999; Kean & Barlow 2004).

The empirical literature on this issue is mixed. Some studies have found that less mobile species are more vulnerable (den Boer 1990; de Vries, den Boer & van Dijk 1996) and some have found that more mobile species are more vulnerable (Gibbs 1998; León-Cortés *et al.* 2003; Van Houtan 2007) to extinction risk due to habitat loss. Thomas (2000) found that butterfly species with intermediate mobility are most vulnerable to habitat loss.

The synthesis presented here (Fig. 2) reconciles these contrasting predictions and findings. Whether species with higher or lower movement probabilities are more or less vulnerable to habitat loss depends on the type of landscape in which the species' movement parameters evolved. For species that evolved either in continuous habitat or in landscapes where the matrix was low-risk (Fig. 2, types A and B), higher movement probabilities and longer movement distances are a

liability when habitat is lost and replaced with high-risk matrix. This prediction was supported in a study of responses of birds to forest removal in the Amazon (Van Houtan *et al.* 2007). The bird species that disappeared from the remaining fragments were those that were most mobile before deforestation occurred. In contrast, for species that evolved in patchy landscapes with high-risk matrix and, particularly for those that evolved in ephemeral habitat with high-risk matrix (Fig. 2, types C and D), higher movement probabilities and longer movement distances are, relatively speaking, an asset when habitat is lost. In scenarios A and B more mobile species experience an increase in movement mortality, whereas in scenarios C and D more mobile species are more likely to find sparsely distributed habitats.

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